PHARYNGEAL TEETH AND SHAPE OF THE *OSSA PHARYNGEA INFERIORA* DURING DEVELOPMENT OF *ABRAMIS BRAMA* (L.) AND *BLICCA BJOERKNA* (L.) (CYPRINIDAE)

by

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ABSTRACT. - The systematic position of bream, *Abramis brama* (Linnaeus, 1758) and white (silver) bream, *Blicca bjoerkna* (Linnaeus, 1758) is still being discussed. This paper presents similarities and differences in the fifth pharyngeal arch of the two species, observed in different stages of development. The arch as well as its pharyngeal teeth are thought to be an important systematic character. Hence, the shape of the arch was examined by analysing the ratio between its width (a) and height (h), as well as by studying characters of the pharyngeal teeth, and especially their formula. Frequency of tooth replacement in prelarvae and larvae was examined by observing the frequency of teeth, present in the tissue surrounding the arch. It was found that the arch width index a/h is different in *A. brama* and *B. bjoerkna* and can be used as a criterion for species classification. Teeth placed in two rows characterize the tooth formula in *A. brama* during a short period of ontogenesis, and part of the adults collected from dam reservoirs. It was found that there is a relationship between the frequency of occurrence of replacement teeth and some characteristic periods of changing tooth formula in *A. brama*. Pharyngeal teeth in adult fish of the two species are replaced continuously, although at a varying rate. Its maximum was observed in summer and autumn.

RÉSUMÉ. - Dents pharyngiennes et conformation des *ossa pharyngea inferiora* pendant le développement de *Abramis brama* (L.) et *Blicca bjoerkna* (L.) (Cyprinidae).

La brème *Abramis brama* (Linnaeus, 1758) et la brème bordelière *Blicca bjoerkna* (Linnaeus, 1758) constituent les espèces dont l'appartenance générique est discutée. Les ressemblances et les différences observées lors du développement du 5ème arc pharyngien ont été suivies à différentes étapes de l'ontogenèse chez ces deux espèces. L'arc, ainsi que les dents pharyngiennes, sont considérés comme un important critère systématique. La forme de l'arc, exprimée par la proportion de sa largeur à la hauteur, la constitution des dents et surtout la formule de la denture ont été examinées. La fréquence du remplacement des dents chez les prélarves et les larves a été étudiée en observant la fréquence de l'apparition des dents de remplacement dans le tissu entourant l'arc. Le remplacement des dents chez les individus adultes a été évalué en tenant compte de la quantité d'alvéoles présentes sur l'arc. On a constaté que l'indice de largeur a/h de l'arc était différent pour *A. brama* et *B. bjoerkna*, et qu'il pouvait être traité comme un critère en systématique. L'existence d'une denture complète à double rangée chez *A. brama* lors d'une courte période de l'ontogenèse ainsi que d'une denture partielle à double rang chez les individus adultes de cette espèce dans les barrages-réservoirs a été confirmée. Il existe une relation entre la fréquence de l'apparition des dents de remplacement et certaines périodes caractéristiques dans le changement de la formule dentaire chez *A. brama*. Le remplacement des dents pharyngiennes chez les individus adultes des deux espèces pendant la durée de ce travail s'est produit continuellement, même si la fréquence n'était pas toujours égale. Le maximum de remplacement se fait en été et en automne.

Key-words. - Cyprinidae, *Abramis brama*, *Blicca bjoerkna*, Poland, Dam reservoirs, Pharyngeal teeth, Replacement teeth, Tooth sockets, Width index.

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According to Nelson (1994), bream, *Abramis brama* (L.), and white (silver) bream, *Blicca bjoerkna* (L.) belong to the order Cypriniformes, family Cyprinidae, subfamily Leuciscinae. Linnaeus (1758) had classified these two species into one genus *Cyprinus* and two species: *Cyprinus brama* and *C. bjoerkna.* The criterion used by Linnaeus (1758) to assign a species to one of the two genera, *Cyprinus* and *Cobitis*, consisted of two characters: presence or lack of barbs, and shape of the caudal fin. Cuvier (1817) introduced a new genus *Abramis* and included *Cyprinus (Abramis) brama* and *C. (Abramis) blicca* into this taxon. Heckel (1842) classified the two species into two different genera based on the number of pharyngeal tooth rows and number and shape of pharyngeal teeth: bream into the genus *Abramis* (teeth in one row), and white bream into the genus *Blicca* (teeth in two rows).

Subsequent studies revealed that bream stocks contained fish having two rows of pharyngeal teeth (Miaskowski, 1960; Shutov, 1967; Lukin, 1971; Suvorova, 1975; Tryapicyna 1979; Golubcov and Ilin, 1983; Tadajewska and Czarkowski, 1994). Shutov (1969), taking into account the presence of the two rows of teeth and type of spawning observed in some females of the two species, proposed to include a monotypical genus *Blicca* into the genus *Abramis*. Shcherbukha (1973) analysed several taxonomic features and also proposed to include the genus *Blicca* into the genus *Abramis*, and to divide the latter into two subgenera: *Ballerus* and *Brama.* The first would comprise *A. (Ballerus) ballerus* and *A. (Ballerus) sapa*, the other *A. (Brama) brama* and *A. (Brama) blicca*. Hensel (1978) concluded on the basis of the sensoric system, shape of the cranium and a high-arched skull that the genus *Abramis* should comprise two species: *A. brama* and *A. bjoerkna*. He distinguished another genus *Ballerus* with the species *B. ballerus* and *B. sapa*. Howes (1981, 1991) studied osteological characters of many cyprinids and their geographic distribution and included not only the genus *Blicca* into the genus *Abramis*, but also the genus *Vimba*. Then he joined the genera *Abramis, Rutilus* and *Chondrostoma* into a lineage *Abramis* in the subfamily Leuciscinae. Boguckaya (1986) used morphological features of the skull and some other bones to suggest that the existing categories of *Abramis, Blicca* and *Vimba* should be maintained. In her later study (1987) she included the mentioned genera as well as the genus *Capaetobrama* into a "group of *Abramis* genera" of the Leuciscinae lineage.

Dubois (1981, 1988) stated in his concept of genus that two species can be included into the same genus if they are able to produce viable and fertile adult hybrids. In natural populations of bream and white bream crosses are quite frequent (Berg, 1949; Zhukov, 1965; Banarescu, 1967; Pushkin, 1971; Swinney and Coles, 1982; Kutuzov, 1983; Witkowski, 1984). The hybrids are fertile and their gonads can be used to determine the sex (Gasowska, 1968), and fertility (Nikolyukin, 1972; Kutuzov, 1983). Experimental studies also confirm fertility of bream and white bream crosses (Nikolyukin, 1972). Taking into account the genus definition presented by Dubois (1981), Howes (1991) and Cavender and Coburn (1993) advocate that two different generic names for species producing viable hybrids is an artefact.

The present paper constitutes part of a more extensive work revising systematic classifications of bream and white bream into one or two genera. Many authors assume that pharyngeal teeth are an important generic character for the taxons belonging to Cyprinidae family (Heckel, 1842; Dybowski, 1862; Günther, 1868; Berg, 1912; Chu, 1935). Cavender and Coburn (1993) even treat them as a synapomorphic feature for the subfamily Phoxininae in their classification of Cyprinidae. The latter cladistic paper deals with cyprinids of North America, and the pharyngeal teeth are considered to be one of the many osteological characters. Pharyngeal bones are also used in feeding studies to determine the size of consumed food items, and together with pharyngeal teeth they are useful in taxonomic paleontological studies. Not only the number of rows, but also the shape of the teeth, their number, and the shape of the arch (pharyngeal jaw) are species-specific (Horoszewicz, 1960).

The number of rows in which the pharyngeal teeth are arranged has been the first character classifying bream and white bream into two genera. A variable number of these rows in bream specimens suggests that the two species might be included into one genus. Hence, it seems that there is a need to establish ontogenetic criteria for the number of pharyngeal tooth rows in bream and white bream in order to reveal similarities and differences that might occur during their development and, then, in adult fish of the two species.

MATERIAL, METHODS AND STUDY AREA

The material consisted of lower pharyngeal jaws of bream and white bream in four stages of development: prelarvae, larvae, fry, and adults. Prelarvae and larvae originated from artificial fish spawning, fry was collected from Zegrze Dam Reservoir, and adults from Zegrze and Sulejów dam reservoirs (Table I). In all stages standard length (SL) was measured. The material from artificial spawing was distinguished in prelarvae and larvae. These were separated by one anatomical feature only. Prelarvae were younger and had not fully formed pharyngeal arches. It was impossible to measure width and length of these. Number of days are expressed as days post-hatching. Age and standard length of bream and white bream prelarvae are presented on figure 1. Age and length of bream larvae were: 66-150 days, SL 11.0-41.7 mm and of white bream larvae: 61-128 days, SL 22.0-32.3 mm.

Zegrze Dam Reservoir is located in middle Poland, 21°E and 52°N. It was constructed in 1962 on the Narew River, a right-hand tributary of the Vistula River. Its area is about 33 km^2, length 60 km, width from 0.5 to 3.0 km. Average depth is 3.5 m, maximal depth, at the dam, is 9 m (Kajak, 1990). Sulejów Dam Reservoir is also located in middle Poland, 20°E and 52°N. It was constructed in 1973 on the Pilica River, a left-hand tributary of the Vistula. Its area is 22.0 km^2, length 15.5 km, width 2.1 km. Average depth is 3.4 m, maximal depth 15.5 m (Galicka *et al.*, 1994). Fish rearing was carried out using juniper as a substrate in concrete tanks 10 x 5 m, in the Experimental Hatchery Dgal of the Inland Fisheries Institute, located in Pieczarki near Gizycko. Fish hatchlings were not fed.

Prelarvae, larvae and fry were preserved in 4% formalin and stained. Combined methods described by Orska (1956), Wassersug (1976), Dingerkus and Uhler (1977) and Rojo (1991) were used to stain bones and cartilage. Pharyngeal jaws were collected from both fresh and preserved fish. In the case of small fish (prelarvae, larvae and fry) the bones were taken out under a stereoscope microscope. Pharyngeal teeth were counted and their formula determined in all stages, and in the case of adult fish attention was paid also to tooth sockets (empty spaces left after a former tooth) noticeable upon the arch (pharyngeal jaw) (Fig. 2). Tooth sockets were treated as a tooth being replaced. In the case of prelarvae and larvae, so-called replacement teeth were also counted, *i.e.* those being formed in the connective tissue around the arch, which later on move to their place on the tooth sockets.

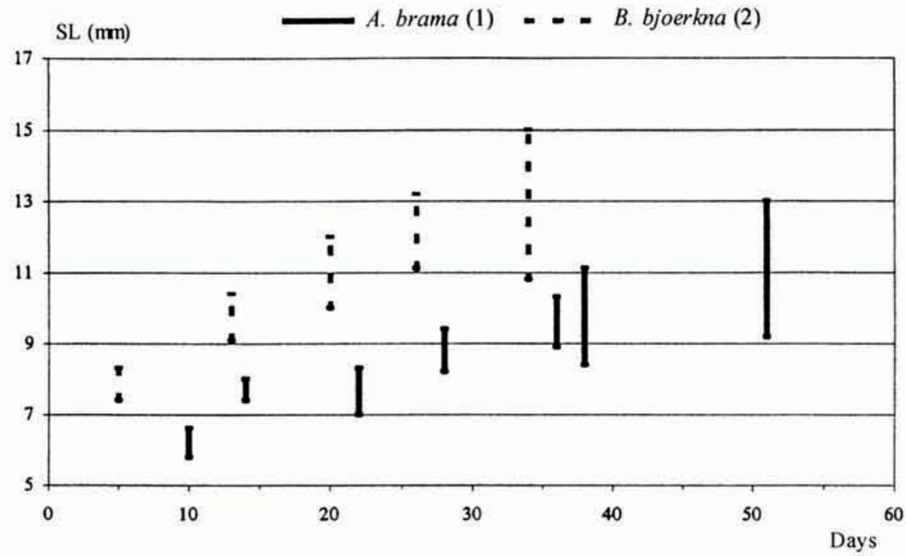


Fig. 1. - Age and standard length (SL) of prelarvae of *Abramis brama* (L.) (1) and *Blicca bjoerkna* (L.) (2) from artificial spawning.

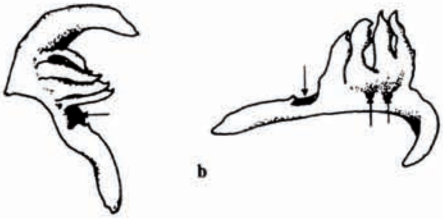
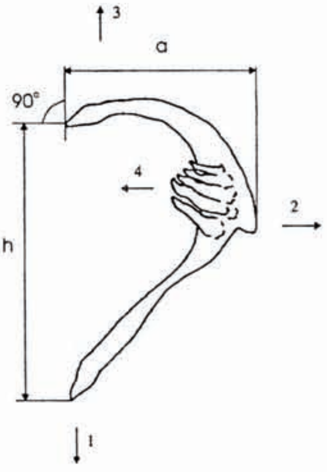


Fig. 2. - Tooth sockets of white bream on left pharyngeal arch. The arrows show sockets. a) Arch seen from above; socket in main row of the teeth; b) Inner lateral side as seen from inside; sockets in main and second rows.

Table I. - Characteristics of the material. SL = length range; * = experimental studies.

	Abramis brama (L.)			*Blicca bjoerkna* (L.)		
Population	**SL (mm)**	**n**	**Date**	**SL (mm)**	**n**	**Date**
Prelarvae *	5.8 - 13.0	63	1 Jun. - 7 Jul. 1994	7.4 - 15.0	26	14 Jun. - 14 Jul. 1995
Larvae *	14.0 - 41.7	60	22 Jul. - 15 Oct. 1994	22.0 - 30.5	45	8 Aug. - 15 Oct. 1994
Fry: **Zegrze Reservoir**	21.0 - 66.0	39	22 Apr. - 15 Oct. 1987	21.0 - 65.0	56	22 Apr. - 15 Oct. 1987
Adults:	178 - 367	40	6 May 1994	157 - 223	18	6 May 1994
Zegrze Reservoir	167 - 322	65	29 Jun. 1994	163 - 268	81	29 Jun. 1994
	173 - 312	39	15 Sep. 1994	186 - 252	35	15 Sep. 1994
Adults:	152 - 370	52	10 Jul. 1993	152 - 266	106	5 Jun. 1993
Sulejów Reservoir	163 - 357	75	17 Apr. 1994	161 - 246	66	17 Apr. 1994
	167 - 324	41	21 Sep. 1994	160 - 248	24	21 Sep. 1994



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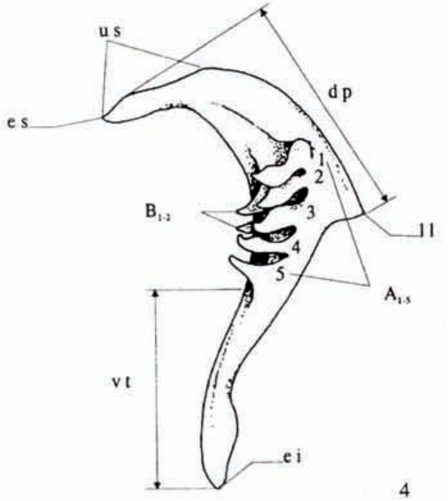

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Fig. 3. - Scheme indicating pharyngeal arch height (h) and width (a) on the right arch of bream. Arch seen from above. 1: anterior; 2: lateral; 3: posterior; 4: medial parts.

Fig. 4. - Description of the right pharyngeal arch of white bream. Arch seen from above: A_{1-5} = main row of teeth; B_{1-2} = second row of teeth; dp = dorsal part; ei = extremitas inferior; es = extremitas superior; ll = lamina lateralis; us = upper section; vt = ventral part.

Height (h) and width (a) of the arch was measured (Fig. 3) up to 0.1 mm. Ratio between arch width and height, was also calculated. It has been called a width index (a/h) and is expressed in percent. When describing particular parts of the pharyngeal arch, the terminology of Horoszewicz (1960) was used (Fig. 4). The location of the upper section has been described according to the same author. This author distinguished 3 positions of the upper arch section. She proposed to place the arch on a horizontal plane divided into 4 quarters by two perpendicular lines (a cross). The arch is placed in such way that its upper end touches the line crossing, while the lower end should touch the vertical line which divides the lower part of the plane into two quarters. Upper location of the arch occurs when the upper section is located in the upper quarter, lower location - when this section is located in the lower half of the plane, while intermediate location occurs when this arch section is located at the borderline between these quarters. Tooth denotations and arrangement of the teeth were taken from Rutte (1962). The shape of the left and right arch was examined in bream and white bream in different stages of development, and in the case of adults attention was also given to the date of sample collection.

The results were subjected to statistical analysis. Tooth formulas for replacement teeth and for tooth sockets were compared using the χ^2 test. To compare arch shape and width index (a/h) obtained in my studies with the literature data, Student's t-test was used. Shape of *ossa pharyngea inferiora* arch was characterised using a linear regression of width (a) and height (h). The differences in arch shape between the samples and the fish species were determined at the significance level $p = 0.05$, verifying the null hypothesis (H_0) on the equality of regression coefficients (test of regression line parallelism), and if necessary, on the equality of intercepts (overlapping of regression lines).

RESULTS

Formation and shape of the arches

In the preparations obtained from the youngest, 10 (5.8-6.6 mm) and 14 (7.4-8.0 mm) -days old bream, the fifth pharyngeal bone (*ossa pharyngea inferiora*) was not fully formed. It was cartilaginous, almost straight in shape, with rounded tips (Fig. $5a_1$). The dorsal part of the arch (*pars dorsalis*) was bigger than the ventral one (*pars ventralis*), there was no sharp, bent upper end (*extremitas superior*), and the lower end (*extremitas inferior*) was not sharp; these characters made the arch quite different from the fully formed one. The middle part, visible under a microscope as a darker area, suggests that the arch fragment in which there were teeth was more dense than the rest. This shape of the arch was still retained in 28-days old bream (8.2-9.4 mm) (Fig. $5a_2$). The ventral part of the arch underwent elongation in the course of subsequent fish growth, as initially this part grew more rapidly than the dorsal one. The middle part became broader forming a lamina (*lamina lateralis*), while the dorsal part bent, attaining a hooked appearance in the final phase (Fig. 5 a_3). Ossification of the arch started from the dorsal to the ventral part. The final shape of the arch became established in bream of about 30 mm (Fig. 6a), although a 21 mm fish with such an arch was also found.

The arch of an adult bream is slender, with both ends sharp, but the upper end is additionally flattened. The dorsal part is characteristically arched. The upper section is lowerly located; this means that in the arrangement as presented in figure 6b the upper section is sloping down. There is a noticeable blunt lateral lamina.

No significant differences were found as to the ratio between arch width and height (a/h) in bream in particular stages of development. Average a/h was from 48.30 to 53.62%, being lower (from 43.30 to 48.96%) in adult fish (Table II).

In 5-days old white bream (7.4-8.3 mm), similarly as in bream, the fifth pharyngeal arch (*ossa pharyngea inferiora*) was not fully formed. In the same way as in the youngest bream, the arch of the white bream is almost straight, but proportions between dorsal and ventral part are variable. The dorsal part (*pars dorsalis*) is almost twice as short as the ventral one (*pars ventralis*) (Fig. 5 b_1, b_2). In subsequent development, the dorsal part of the white bream arch clearly bends and elongates (Fig. 5 b_3, b_4, b_5). As in bream, the middle part is broader and forms a lamina (*lamina lateralis*), but it is noticeably broader than in bream. Ossification proceeds similarly as in bream. The arch attains its final shape in fish about 30 mm long (Fig. 6c).

The arch of an adult fish is broader and more massive than in bream. The upper end is distended, and the lower end slightly truncated. The lateral lamina is hooked and sharp. The upper section is lowerly located (Fig. 6d).

White bream was characterised by a higher disproportion of the ratio between arch width and height (a/h) in particular stages of development. It ranged from 56.79 to 65.99%, but in adult fish it was 64.25 to 65.99% (Table. II).

Statistical analysis of the error values of the mean estimates (SEM) of arch width index a/h (Table II) revealed that they were not too high. Hence, the materials were not too differentiated, and it was possible to compare average a/h index between bream and white bream. In almost every case the results for bream were significantly lower than for white bream ($p < 0.05$), larval stages being the only exception. This suggests that the index of arch width may have a diagnostic value for these two fish species. In view of this, it was decided to compare not only the mean values, but also a/h relation in the form of regression lines. Since no significant differences were found between the left and the

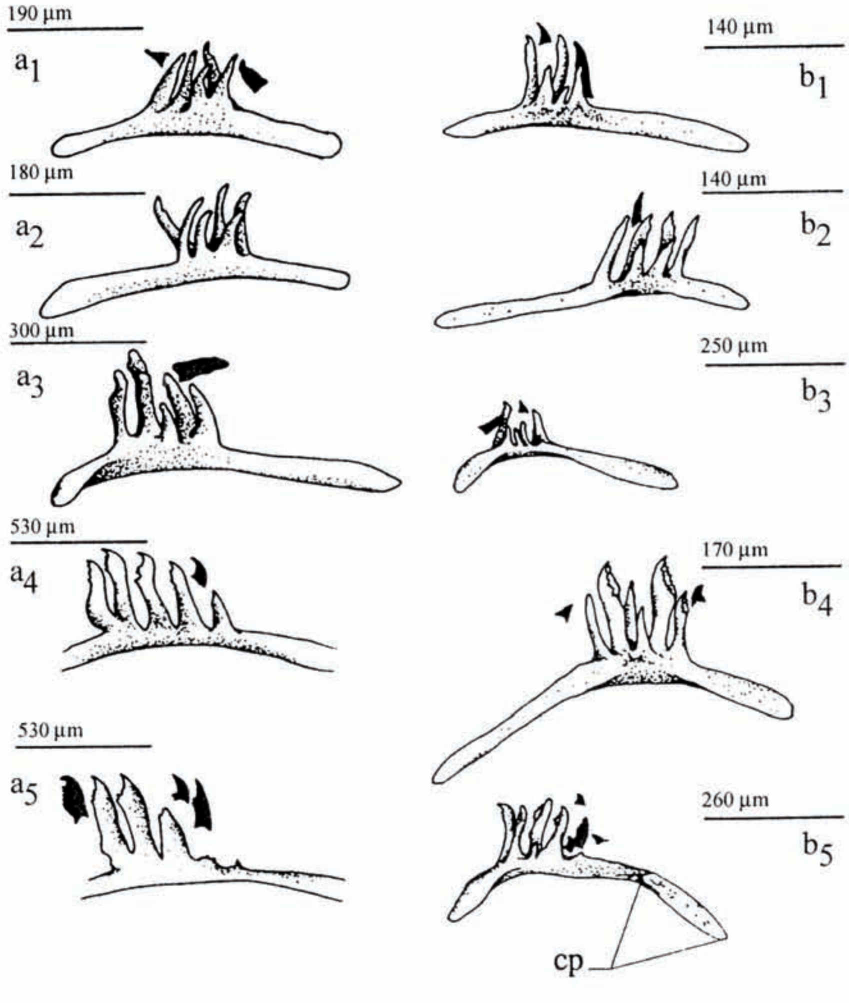


Fig. 5. - Pharyngeal arch and teeth in *Abramis brama* (L.) (a) and *Blicca bjoerkna* (L.) (b) in early stages of development. Replacement teeth are shaded: os.ph. = tooth formula; SL = standard length.
Abramis brama (L.): a_1 right arch, SL 7.0 mm, os. ph 3.2; a_2 left arch, 8.0 mm, os. ph 3.3; a_3 right arch, 10.3 mm, os. ph 4.2; a_4 middle part of right arch, 13.0 mm, os. ph 5; a_5 middle part of right arch, 9.9 mm, os. ph 3.
Blicca bjoerkna (L.): b_1 right arch, SL 7.4 mm, os. ph 2.3; b_2 left arch, 8.3 mm, os. ph 2.4; b_3 right arch, 10.4 mm, os. ph 3.2; b_4 left arch, 10.6 mm, os. ph 1.5; b_5 right arch, SL 10.9 mm, os. ph 4.1; cp = cartilage part.

right arch in different stages of development ($p > 0.05$) the results for the two arches were combined in the subsequent analyses.

The linear regressions for the relationship between arch width (a) and height (h) in bream and white bream in different stages of development are presented in figure 7. Correlation between a and h proved to be highly significant. Comparison of regression lines

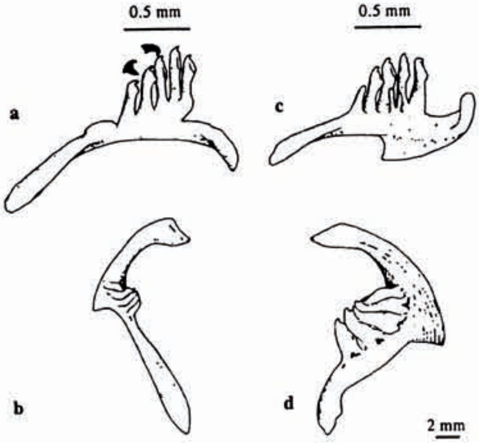


Fig. 6. - Fully formed pharyngeal arch of larvae *Abramis brama* (L.) (a) and of adult *Abramis brama* (b) and of larvae *Blicca bjoerkna* (L.) (c) and of adult *Blicca bjoerkna* (L.) (d): SL = standard length; os.ph. = tooth formula; h = height; a = width; a/h = width index.
a) left arch - SL 29.3 mm, os.ph 5, h = 3.5 mm, a = 1.8 mm, a/h = 51.42%.
b) left arch - SL 276 mm, os.ph 2.5, h = 1.7 mm, a = 1.1 mm, a/h = 64.70%.
c) left arch - SL 23.3 mm, h = 18.3 mm, a = 9.2 mm, a/h = 50.3%.
d) right arch - SL 231 mm, h = 17.7 mm, a = 11.9 mm, a/h = 67.2%.

for the two fish species (Fig. 7) suggests that in early stages of development (larvae and fry) width and height increments show similar trends both in bream and white bream. In the case of adult fish increments of arch width in relation to height were greater in white bream than in bream, the differences being statistically significant.

Comparison of regression lines between different dates of bream and white bream sampling in Zegrze and Sulejów reservoirs showed that the results obtained for bream from Zegrze Reservoir differed from those for white bream. In bream originating from this reservoir, increment of width with height growth was similar in all sampling periods. In white bream this was not the case - comparisons of May with June, and of May with September differ significantly ($p < 0.05$) from the comparison of June with September,

Table II. - Comparison of the mean values of width index (in %) for pharyngeal arch of *Abramis brama* (L.) and *Blicca bjoerkna* (L.) based on the literature and own data. The results of Student's t test: p = level of significance; x = mean; SEM = standard error mean; ^{x} = Horoszewicz, 1960; ^{xx} = Krzykawski and Gawlinski, 1986; * = significant difference.

	Abramis brama (L.)		*Blicca bjoerkna* (L.)		Comparison
Population	n	x ± SEM	n	x ± SEM	**of species**
Larvae	60	51.71 ± 4.36	45	62.55 ± 3.20	$p > 0.05$
Fry	39	53.62 ± 6.21	56	56.79 ± 5.20	$p < 0.05$ *
Zegrze Reservoir	144	48.96 ± 2.15	134	64.25 ± 3.26	$p < 0.05$ *
Sulejów Reservoir	168	48.30 ± 2.08	196	65.99 ± 3.45	$p < 0.05$ *
Vistula River ^{x}	39	47.90 ± 4.36	33	62.50 ± 4.75	$p > 0.05$
Dabie Lake ^{xx}	33	51.88 ± 3.30	36	68.77 ± 8.13	$p < 0.05$ *

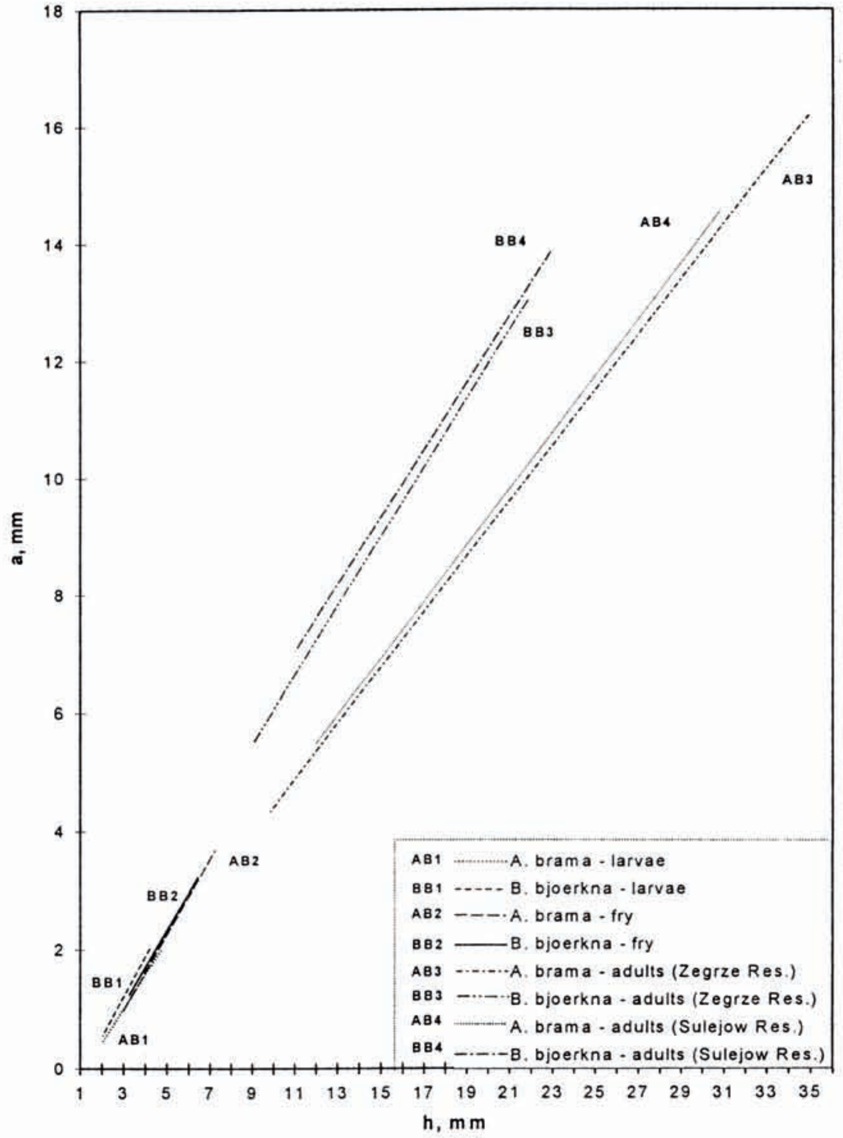


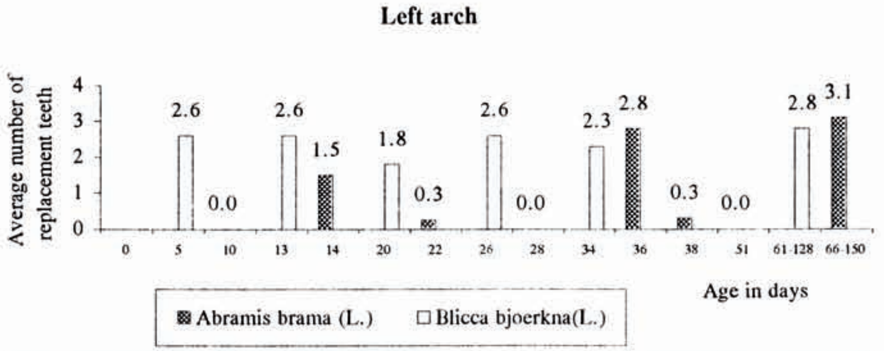
Fig. 7. - Relationship (regression equation) between arch width (a) and height (h) in *Abramis brama* (L.) and *Blicca bjoerkna* (L.) in particular stages of development. AB1: $r^2 = 0.94$, $y = 0.56x - 0.08$; BB1: $r^2 = 0.70$, $y = 0.53x + 0.19$; AB2: $r^2 = 0.92$, $y = 0.67x - 0.43$; BB2: $r^2 = 0.88$, $y = 0.62x - 0.14$; AB3: $r^2 = 0.92$, $y = 0.48\,x + 0.29$; BB3: $r^2 = 0.84$, $y = 0.58x + 0.83$; AB4: $r^2 = 0.96$, $y = 0.48x + 0{,}10$; BB4: $r^2 = 0.88$, $y = 0.58x + 1.24$. All r^2 coefficients are statistically significant ($p < 0.05$).

when the regression lines overlapped. In Sulejów Reservoir no significant differences were found between samplings, both in the case of bream and white bream (regression lines were parallel or overlapped).

Table III. - Distribution of various tooth formulas in *Abramis brama* (L.) and *Blicca bjoerkna* (L.) in the examined stages of development (in%).

	Abramis brama										
	Prelarvae							Larvae	Fry	Adults Sulejow	Adults Zegrze
	Body length (SL) in mm										
Tooth formula	5.8 - 6.6	7.4 - 8.0	7.0 - 8.3	8.2 - 9.4	8.9 - 10.3	8.4 - 11.1	9.2 - 13.0	11.0 - 41.7	21.0 - 66.0	152 -370	167 -367
2-2	33.3										
3-3	66.7	100.0					4.8				
4-4							42.9				
4-5							19.0	1.7			
5-4							14.3		2.6	1.8	
5-5							19.0	68.3	89.6	85.1	95.1
5-6								3.3			
6-5								26.7			0.7
3-3.3				9.1							
4-4.1					20.0						
4-4.2					20.0						
5-5.1										6.0	2.1
1.3-3			12.5								
1.5-5									2.6	4.2	1.4
2.5-4									2.6		
1.2-2.1			12.5								
1.2-2.2			12.5								
2.2-2.2			25.0								
1.3-3.1						11.1					
2.3-3.1				9.1							
2.3-3.2			37.5			44.5					
2.3-3.3				9.1							
2.3-3.4				9.1		11.1					
3.3-3.2				18.2							
3.3-3.3				36.3							
4.3-3.4				9.1							
2.4-4.2					60.0	33.3					
1.5-5.1										2.9	0.7
2.5-5.1									2.6		
n	3	6	8	11	5	9	21	60	39	168	144

	Blicca bjoerkna								
	Prelarvae					Larvae	Fry	Adults Sulejow	Adults Zegrze
	Body length (SL) in mm								
Tooth formula	7.4- 8.3	9.1- 10.4	10.0- 12.0	11.1- 13.2	10.8- 15.0	22.0- 32.3	21.0- 65.0	152-266	157-268
4-3		20.0							
4-4		40.0							
5-3							1.8		
5-5						6.7	25.0	0.5	0.7
5-5.2						2.2			
5-5.3							1.8		2.2
1.5-4				20.0					
1.5-5						2.2			
2.5-5						4.4			
2.2-2.3	20.0								
1.3-2.1	20.0								
1.3-3.1	40.0								
1.4-3.2		20.							
2.4-2.2	20.0								
2.4-4.1				20.0					
2.4-5.2									1.5
1.5-4.1			40.0	40.0					
1.5-5.1						6.7	5.3	1.0	5.2
1.5-5.2						11.1		3.6	6.7
2.5-4.1			20.0						
2.5-4.2			40.0		66.7			1.5	3.0
2.5-5.1		20.0		20.0		13.3	1.8	3.0	5.2
2.5-5.2					33.3	53.3	62.5	89.4	73.1
2.5-5.3									0.7
3.5-5.2							1.8	1.0	0.7
3.5-5.3									0.7
n	5	5	5	5	26	45	56	196	134



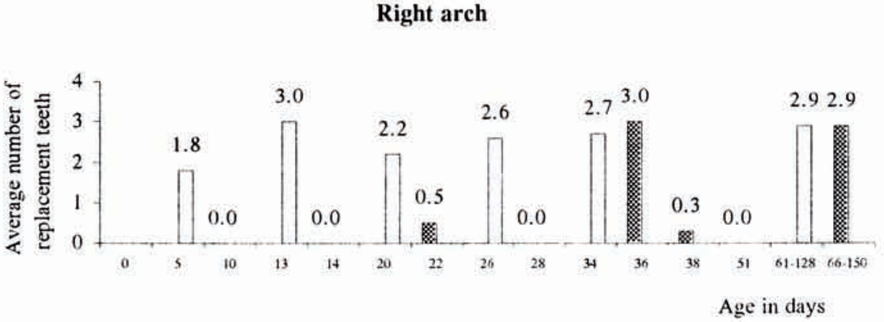


Fig. 8. - Average number of replacement teeth in right and left arch of prelarvae and larvae of *Abramis brama* (L.) and *Blicca bjoerkna* (L.).

Development and shape of teeth

The first teeth in bream (the so-called primary teeth) appear as early as in 10-days old specimens (5.8-6.6 mm; possibly even earlier), when the arch is not yet fully formed; usually two or three teeth are present on the left and the right arch (Table III). They are pointed, of almost the same height, and bent slightly backwards. The secondary teeth of the first generation in the main row are similar in shape and size to the primary ones. They appear in bream of 22 days old (7.0-8.3 mm). Between day 22 (7.0-8.3 mm) and day 38 (8.4-11.1 mm) they occur together with the primary teeth (period of two rows) (Fig. 5 a_1, a_2, a_3). The primary teeth are gradually lost between day 22 (7.0-8.3 mm) and 50 (9.1-13.0 mm).

White bream aged 5 days (7.4-11.1 mm) also has teeth on not yet fully formed arch, the main row having 2 to 4 teeth, and the second row 1 to 3 (Table III). Their shape and size is quite different. Teeth in the main row are noticeably higher than teeth in the second row. They look very much like the teeth of the first generation (secondary teeth) in bream, or even the subsequent ones. Shape and size of teeth in the second row resemble primary teeth of bream, but they are not bent (Fig. 5 b_1, b_2, b_3).

Both in bream and white bream the teeth of the next generations of secondary teeth are formed beyond the arch, in the surrounding connective tissue, and they gradually grow towards the arch. The middle teeth (second and third) are the first to take their place, followed by the fourth, and then the first and fifth. Secondary teeth are noticeably higher than primary, and their shape differs in particular stages of development (Fig. 5). A

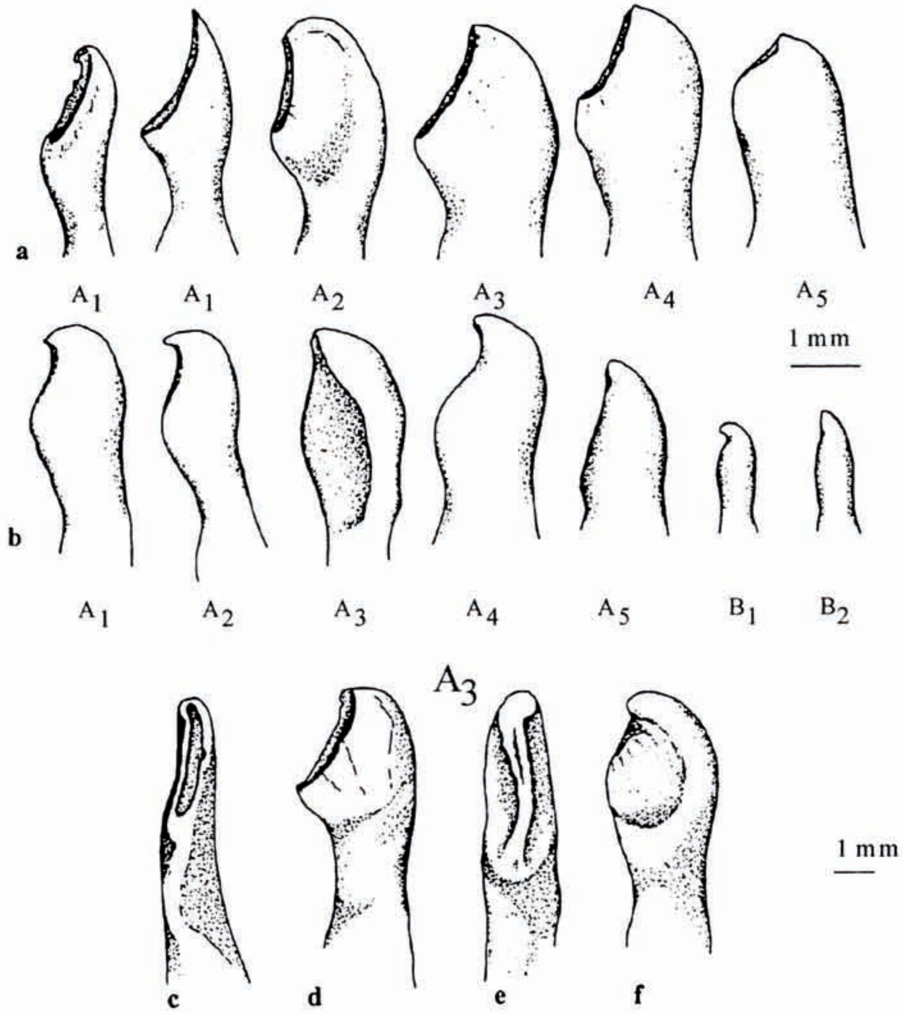


Fig. 9. - Teeth of adult *Abramis brama* (L.) (a) and *Blicca bjoerkna* (L.) (b) and A_3 tooth of *Abramis brama* (L.) (c: frontal view; d: ventral view) and *Blicca bjoerkna* (L.) (e: frontal view; f: ventral view).

secondary tooth appears first in the form of a more or less acute triangle, then its neck extends. Folds and grooves appear upon its crown, thereby increasing the masticating surface (Fig. 5 a_4, b_5). Teeth that are formed in this way and move into their respective places have been called the replacement teeth.

In bream prelarvae and larvae the replacement teeth were less numerous and occurred less frequently than in white bream. Bream prelarvae had from 1 to 4 replacement teeth, usually 1 tooth on 17.5% (right) and 25.4% (left) of the examined arches (jaws). In bream larvae these teeth were observed in already 56.7% of the arches (with the same frequency in right and left jaw). Their number ranged from 1 to 5, usually 3. In white bream replacement teeth were found in all prelarvae and larvae examined: from 1 to 4, usually 2 in prelarvae, and from 1 to 5, usually 3 in larvae.

Average numbers of replacement teeth on the left and right arch of early developmental stages of bream and white bream are presented in figure 8. In the case of bream prelarvae there were periods when no replacement teeth were found [days 10 (5.8-6.6 mm), 28 (8.2-9.4 mm), 51 (9.2-13.0 mm)], and periods when these teeth were very frequent [days 14 (7.4-8.0 mm), 36 (8.9-10.3 mm) and larval stage (11.0-41.7 mm)]. On the other hand, these teeth were always found in white bream, and their average number in prelarvae ranged from 1.8 to 3.0, the mean being 2.5. In white bream prelarvae the replacement teeth were 5 times more frequent than in bream, but in the case of larvae no greater differences in the average number of replacement teeth were observed between the two species.

Teeth of adult bream (Fig. 9a A_1-A_5) were cylindrical in shape and slightly S-bent. Their crowns were flat and compressed. All had a masticating surface, the size of which reached 2/5 of the tooth length. The masticating surface was narrow (Fig. 9c). The hooked and sharp A_1 tooth was more slender and less massive than the other teeth. The A_2 and A_3 teeth were either hooked or blunt at the tip, depending on the degree of their wearing out. The A_4 tooth was blunt at the tip, but its crown was more compressed than of the A_3 tooth. The A_5 tooth was the most cylindrical in shape, flatly truncated, with the smallest masticating surface.

Teeth of adult white bream (Fig. 9b A_1-A_5, B_1-B_2) form two rows. Those in the first row are more massive and more strongly compressed than in bream. They have noticeable, sharp hooks; their crown is flat, and the masticating surface is as big as in bream, but narrower and longer. There is a noticeable groove on the masticating surface (Fig. 9e). The A_1-A_4 teeth have hooked tips. The A_5 tooth has a cone-shaped tip. Teeth of the second row are located upon the jaw (arch) between the A_2 and A_3 tooth. They are noticeably lower than teeth in the main row. The B_1 tooth has a hooked tip, while the tip of the B_2 tooth is blunt.

The location of the teeth upon the arch of adult bream and white bream is quite different. Teeth of bream occupy a much smaller section in the middle part of the jaw, limited by the lateral lamina, whereas in white bream they occupy an area almost twice as large (Fig. 6d).

Tooth replacement in adult fish

The number of tooth sockets was examined separately for the left and right pharyngeal jaw in the period from April to September in adult bream and white bream (Table IV).

It was found that in both species the teeth were replaced throughout the whole observation period, though with different frequency. In bream tooth replacement was less intensive in April and May compared to the subsequent months. Samples collected in this period from Zegrze and Sulejów reservoirs contained relatively low percentages of jaws with empty tooth sockets (from 6.7 to 8.0% of all jaws examined). The most intensive tooth replacement took place in June (tooth sockets found in 38.5-40.0% of the examined arches).

In white bream (Table IV), as in bream, relatively few tooth sockets were observed in April and May, both in the first and the second rows. Tooth sockets were observed in this period in maximally 6.1% of the examined arches, suggesting low levels of replacement. At the end of June, the intensity of tooth replacement was already high and remained fairly high until autumn.

During intensive tooth replacement (summer, autumn) maximally two tooth sockets were observed upon one arch of bream, and three upon one arch of white bream. There was only one case when four tooth sockets were found in white bream.

Analysing statistical distribution of tooth sockets present in adult bream and white bream from the two reservoirs in different sampling periods, and comparing left with right arch it was found that arches (left versus right) did not differ in a significant way. The only exception for bream was September in Sulejów Reservoir, and for white bream June and September in Zegrze Reservoir, but only in the main tooth row. Tooth socket distribution examined on the jaws of bream and white bream from the two reservoirs, and comparison of the sampling periods revealed that the intensity of tooth replacement was similar in both reservoirs. In summer (June, August) and autumn (September) it was more intensive than in spring (April, May), and the differences were statistically significant. There were, however, no statistically significant differences between summer and autumn.

Formula of pharyngeal teeth

In the youngest bream [10 (5.8-6.6 mm) and 14 (7.4-8.0 mm) days] originating from artificial spawning the pharyngeal teeth were arranged in one row of the formula 2-2 or 3-3. During a short period, when the fish were aged 22 (7.0-8.3 mm) to 38 (8.4-11.1 mm) days, teeth were arranged in two rows in a very differentiated way (16 types of

Table IV. - Location and frequency of tooth sockets upon left (L) and right (R) arch of adult *Abramis brama* (L.) and *Blicca bjoerkna* (L.) on the dates of collection. A_{1-5} = teeth of the main row; B_{1-2} = teeth of the second row; n = number of tooth sockets; n_1 = number of arches with tooth sockets; n_2 = number of examined arches.

	Zegrze Reservoir						**Sulejów Reservoir**					
	***Abramis brama* (L.)**											
	6 May 1994		29 Jun. 1994		15 Sep. 1994		10 Jul. 1993		17 Apr. 1994		21 Sep. 1994	
Tooth	L	R	L	R	L	R	L	R	L	R	L	R
Σ **n** A_{1-5}	3	3	34	27	15	15	12	12	6	5	10	20
n_1	3	3	26	25	13	13	12	12	6	5	10	17
n_2	40	40	65	65	39	39	52	52	75	75	41	41
%	7.5	7.5	40.0	38.5	33.3	33.3	23.1	23.1	8.0	6.7	24.4	41.5
	***Blicca bjoerkna* (L.)**											
	6 May 1994		29 Jun. 1994		15 Sep. 1994		5 Jun. 1993		17 Apr. 1994		21 Sep. 1994	
Σ **n** A_{1-5}	0	1	40	27	15	7	11	18	3	4	5	3
n_1	0	1	32	23	14	7	11	18	3	4	4	3
n_2	18	18	81	81	35	35	106	106	66	66	24	24
%	0	5.6	39.5	28.4	40.0	20.0	10.4	17.0	4.5	6.1	20.8	12.5
Σ **n** B_{1-2}	1	1	13	19	8	8	11	9	4	2	2	4
n_1	1	1	13	16	7	6	10	9	4	2	2	3
n_2	18	18	81	81	35	35	106	106	66	66	24	24
%	5.6	5.6	16.0	19.7	20.0	17.1	9.4	8.5	6.1	3.0	8.3	12.5

teeth formula). Fish aged 51-150 days (9.2-41.7 mm) had again only one row of pharyngeal teeth (Table III).

The most common, symmetrical formula of pharyngeal teeth in bream, *i.e.* 5-5, appeared only in fish aged 51 (9.2-13.0 mm) days, when 19% of the specimens were characterised by this formula. As the fish grew, frequency of this formula increased. Experimentally-reared bream aged 66-150 days (11.0-41.7 mm) conformed to this formula in 68.3% of the fish. In bream fry originating from a natural population, 21.0-66.0 mm fish had pharyngeal teeth arranged in either one or two rows. The 5-5 formula occurred in 89.6% of the fish. Teeth in two rows were found in 7.8% of the fish. In adult bream from Zegrze and Sulejów reservoirs, the formula 5-5 was the most frequent one (in 95.1 and 85.1% of the fish respectively). A small percentage of the fish had their teeth arranged in two rows. In most of these cases the second row contained only one tooth, either on the right or on the left arch. Some fish had teeth of the formula 1.5-5.1: 0.7% in Zegrze Reservoir, and 3.0% in Sulejów Reservoir (Table III).

Anomalies in bream tooth formula are presented in figure 10. There is an additional sixth tooth (A_6) on the first arch (a), and there is one tooth in the second row (formula 1.5) on the second arch (b).

Two rows of teeth were usually observed in all stages of development of white bream, although sometimes the teeth were arranged in one row only. A relatively high percentage of specimens with teeth placed in one row (26.8%) was observed in fry from a natural population (Table III). The most frequent formula in the case of teeth placed in one row was 5-5. In the youngest white bream (5 days; 7.4-8.3 mm) only specimens with teeth placed in two rows were found. Similarly as in young bream, the main row contained only two or three teeth. The first and fifth tooth appeared in later stages of fish development, the fifth tooth appearing first on the left arch.

The tooth formula most typical of white bream, viz. 2.5-5.2, appeared for the first time in fish aged 34 days (10.8-15.0 mm), when it was observed in 33.3% of the examined specimens. Frequency of this symmetrical formula increased along with individual development. In white bream aged 61-128 days and size 22.0-32.3 mm, up to 53.3% had this formula, and in a natural fry population of fish 21.0-65.0 mm long, up to 62.5%. The latter value may be underestimated, as the examined sample might have comprised some bream (having teeth in one row). The above two groups of fish had five teeth in the main row, and the differences concerned teeth in the second row, in which some teeth were missing, or there were some extra teeth in the right or left arch.

In adult white bream a typical 2.5-5.2 formula was present in 89.29% of the examined fish originating from Sulejów Reservoir, and in 73.12% of fish from Zegrze Reservoir. Considerable differences in tooth formula in the remaining fish resulted not only from the differences in tooth numbers in the second, but also in the first row. A lack of, or some extra teeth in the second row of right or left arch were found in 9.22% of white bream from Sulejów Reservoir, and 22.40% of the fish from Zegrze Reservoir. Four teeth in the main row of the right or left arch were observed in 1.53% of the white bream from Sulejów Reservoir, and 4.48% from Zegrze Reservoir (Table III).

Examples of anomalies in tooth arrangement in white bream are presented in figure 10. Teeth are present in one row on the first arch (c) only, and there are three teeth in the second row on the second arch (d) (formula 3.5).

Examining statistical distribution of tooth formulas and of replacement teeth on left and right arch of bream and white bream in different stages of development, reveals that significant differences can be noted only with respect to tooth formula in bream

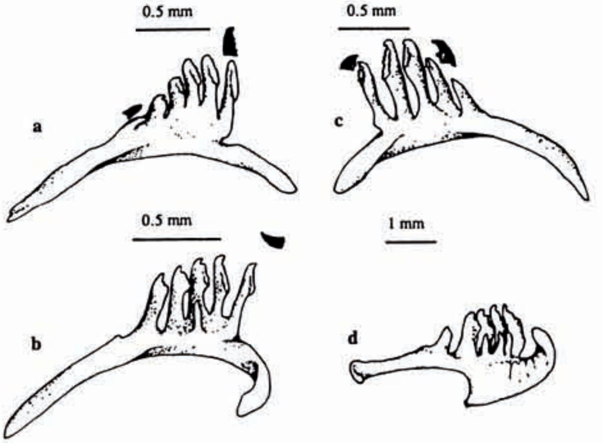


Fig. 10. - Anomalies in tooth formula in *Abramis brama* (L.) (a,b) and *Blicca bjoerkna* (L.) (c,d) larvae and fry. SL = standard length; os.ph. = tooth formula; h = height; a = width; a/h = width index.
a) left arch - SL 27.5 mm, os. ph 6, h = 2.3 mm, a = 1.2 mm, a/h = 52.17%
b) left arch - SL 21.0 mm, os. ph 1.5, h = 1.7 mm, a = 0.9 mm, a/h = 52.94%
c) right arch - SL 23.1 mm, os.ph 5, h = 1.8 mm, a = 1.1 mm, a/h = 62.86%
d) left arch - SL 54.0 mm, os. ph 3.5, h = 4.2 mm, a = 2.7 mm, a/h = 64.28%

larvae. There are no significant differences between the arches in other stages of bream development. In the case of white bream, significant differences are observed only in the prelarval stage. As regards the replacement teeth, there were no significant differences between left and right arch of bream and white bream prelarvae and larvae.

Comparing the distribution of tooth formulas between the developmental stages of bream and white bream and with left and right arches taken together, it can be concluded that they differ in a significant way ($p < 0.05$) in all variants. The only exceptions were when bream fry was compared with adults from Zegrze Reservoir, and when bream adults were compared between the two reservoirs. There were no similarities in tooth formula between bream and white bream in all stages of individual development ($p = 0.0000$).

DISCUSSION

The relevant literature contains little information on the formation of the pharyngeal arch (*ossa pharyngea inferiora*) and its teeth in the species from the family Cyprinidae (Bielogurov, 1957; Horoszewicz, 1960; Urbanowicz, 1960; Eastman and Underhill, 1973; Prawocheński, 1974; Vandewalle *et al.*, 1992, 1994). Vandewalle *et al.* (1992) stated that the fifth pharyngeal arch in *Barbus barbus* appeared on the seventh day of life, at body length 9.9 mm, being the last gill arch to appear. During subsequent development it became elongated, bended, and ossified. The tooth plate (of dermal origin) usually appeared as the first bony element of the arch (Vandewalle *et al.*, 1994). The results of my studies show that this process was very similar in bream and white bream. The arches attain their final shape at a fish length of 30 mm. Fully formed arches of the two species differ with respect to their solidity and width. The pharyngeal arch of white bream is more massive and broader than that of bream. The arch shape reflected in the width index (ratio between arch width and height) oscillates in adult *A. brama* around an average of 50%, and in *B. bjoerkna* around 65%. These differences confirm the results of earlier studies on bream populations in Goczalkowice Dam Reservoir (50.83%), Czchów Dam Reservoir (51.71%), Vistula Lagoon (53.05%), and at six stations along the Vistula River (50.65-51.93%) (Tadajewska and Czarkowski, 1994). Data presented for bream (47.90%) and white bream (62.50%) by Horoszewicz (1960), and for bream (51.88%) and white bream (68.77%) by Krzykawski and Gawliñski (1986) show the same trend. Consequently, arch shape expressed in the width index may be used as a diagnostic character for the two species.

Frequency of replacement tooth appearance in prelarvae and larvae differs in bream and white bream. Periods of increased occurrence of these teeth are related to tooth formation. Four such periods were distinguished in bream in my previous studies: first at the fish age of up to 14 days (7.4-8.0 mm), when primary teeth appear on the arch in one row; second at the age of 22-38 days (7.0-11.1 mm), when two rows of teeth develop as a result of a new generation of teeth appearing next to the primary teeth. This new generation later on forms the main row. The third period is observed in fish aged 39-50 days (9.2-13.0 mm), when primary teeth are lost, so that bream have again only one row of pharyngeal teeth. The number of teeth in the main row gradually increases in this period up to 5, and secondary teeth appear with masticating surfaces on teeth A_2-A_4. The fourth period, at fish length 11.0-41.7 mm, ends the process of tooth formation, so that they attain the final formula. According to Bielogurov (1957), two rows of teeth appear at bream length 7-11 mm and remain there until the fish attain 20 mm. This author also showed that there was a brief period in bream ontogenesis when the pharyngeal arch bore three rows of teeth. My studies confirmed the fact that there were two rows of teeth during bream ontogenesis, at the fish length given by Bielogurov (1957), only one row in fish 9.2-13.0 mm, but did not confirm the presence of three rows. The first two teeth and then a third one appear on the arch between days 12 and 16. In other cyprinids like *Chondrostoma nasus* (Prawocheñski, 1974; Vandewalle *et al.*, 1992) and *Cyprinus carpio* (Bielogurov, 1957), they appear at body length 5-9 mm, this range being also close to my own results. Bielogurov (1957) also determined the period during which teeth in bream changed to their final form: this occured in fish 23-57 mm long (A_2-A_5 teeth). He furthermore stated that there were 6-8 tooth generations before this period. Tooth shape in this size range has not been examined in this study, but the presence of many replacement teeth on both arches (2.9 and 3.1 on the average) in larvae of 11.0-41.7 mm length suggests a high intensity of tooth replacement in this period of bream life. This would also correspond to the period defined by Bielogurov (1957) as the period of final tooth formation.

It was not possible to distinguish the respective periods of tooth formation in white bream because the numbers of replacement teeth, and number of tooth rows on the arches remained at an almost unchanged level throughout the study period. This would point to potentially greater and more stable replacement of teeth in white bream compared to bream. Secondary teeth with masticating surfaces appeared in white bream aged 20 days, at a body length of 10.0-12.0 mm. No literature has been found discussing the appearance of pharyngeal teeth in *B. bjoerkna*.

Data on the frequency of tooth replacement in adult fish are scarce and controversial. Prawocheñski (1974) examined replacement of teeth in *Chondrostoma nasus* and stated that it was not systematic and depended on how much the teeth were worn out. Teeth located in the middle, most intensively used area, were replaced more frequently, and the maximum rate of replacement was observed in autumn and the beginning of winter. According to Rutte (1962) teeth were regularly replaced in cyprinids, irrespective of their use. Evans and Deubler (1955) studied two cyprinid species, *Semotilus atromaculatus* and *Clinostomus elongatus* and found that teeth were replaced throughout the whole life, with different frequency, and in a definite sequence on both arches (5-3-1-4-2).

Studies by Urbanowicz (1960) showed that teeth in adult *Leucaspius delineatus* were replaced all year round, at the highest rate from May till August, but consecutive teeth were not replaced simultaneously. My studies confirm those of Urbanowicz (1960). Some shift in time results from different methods of examining the process of tooth replacement. This author defined the intensity of replacement by counting the replacement teeth, which appeared before the actual succession. Golubcov and Ilin (1983) too confirmed that the replacement rate was the highest in August and September.

Pharyngeal teeth play an important role in cyprinid feeding (Evans and Deubler, 1955, Horoszewicz, 1960; Rutte, 1962; Sibbing, 1982, 1988; Ritterbusch-Nauwerck, 1990), and their shape is related to their function and the type of food organisms ingested by particular species. Arches, as well as pharyngeal teeth of bream and white bream differ considerably. The big and strong teeth of white bream, growing on massive arches suggest that their function is different from that of the smaller and more delicate bream teeth, growing on thinner arches. Simple comparison of fish diets in the same water bodies shows that bream prefers Chironomidae larvae, planktonic crustaceans (Cladocera, Copepoda) and bottom crustaceans (Ostracoda). White bream also prefers Chironomidae larvae, but more frequently the species feeds on littoral vegetation (*Isocladius silvestris, Parachironomus varus, Endochironomus tendens, Gliptotendipes gripekoveni*) and molluscs (*Bithynia sp., Valvata,* Sphaeriidae) (Wielgosz and Tadajewska, 1988; Tadajewska, 1993).

Bream and white bream, which at first both inhabit the littoral zone, at a certain stage of life separate their feeding niches. The results of detailed studies on the filtering apparatus of bream and white bream (Lammens, 1984; Lammens *et al.*, 1987; Berg *et al.*, 1994) revealed that the apparatus of bream was more effective than that of white bream. Bream can filter plankton more effectively due to a much bigger filterring area and performance of the filtering apparatus thanks to special muscles which decrease gaps between the gill rakers. This greatly improves its retention ability for smaller prey. White bream has no such abilities. Consequently, white bream must commence feeding on bigger organisms and benthos earlier in life than bream; it is also more effective in this type of food uptake than bream. Lammens (1984) explained the presence of big bream specimens in the open water zone by the presence of zooplankton composed of small organisms, as well as by the substrate made up of small particles and small chironomids. Berg *et al.* (1994) confirmed that the branchial sieve of bream is better adapted to exploit both zooplankton and chironomid larvae efficiently. Martyniak (1993) showed that big bream fed in deeper waters, in the water column from the bottom to the surface. These studies and the discovery of the role played by mucus in food transportation from the filtering apparatus (Hoogenboezem and Boogaart, 1993) point to the relationship between architecture of the pharyngeal teeth and feeding behaviour of the two species. In the long period during which bream feeds mostly on soft food and plankton, it does not require strong teeth. Their function is limited to squeezing and compressing the food bolus. Large bream which feeds on benthic fauna possesses pharyngeal teeth strong enough, albeit delicate, to crush the substrate or even mollusc shells. White bream feeds on plankton only for a brief period of early life, and stays closer to the shores for the rest of its life. Here, it mostly feeds on benthic organisms separating them from the coarse substrate, or on fauna developing on the aquatic plants. This type of food requires stronger teeth already in relatively small fish, able to crush and masticate the substrate, and white bream teeth are adapted to this function.

The number of rows of pharyngeal teeth is considered to be an important diagnostic character of cyprinid species. At first it was thought that bream has only one row, and white bream two rows of teeth (Heckel, 1842). When it was found that there were bream populations having two rows of pharyngeal teeth, *i.e.* that this character is subjected to intraspecific variations, its validity in distinguishing the genera *Abramis* and *Blicca* became doubtful. Cavender and Coburn (1993) advocate that this character might have undergone a reversal in the course of cyprinid evolution, whereby its use in establishing the similarities between these fish becomes highly limited. Subsequent studies determined the frequency of a tooth formula composed of teeth placed in two rows (Table V). The fraction of fish with such a tooth formula in bream populations was estimated to range from 1.5 to 10% (Miaskowski, 1960; Tryapicyna, 1979; Krzykawski and Gawliñski, 1986; Tadajewska and Czarkowski, 1994), and from 10 to 20% (Shutov, 1967; Lukin, 1971; Suvorova, 1975; Sappo, 1976; Golubcov and Ilin, 1983). In my studies this formula of pharyngeal teeth was found in 4.2% of adult bream in Zegrze Dam Reservoir and 13.1% in Sulejów Reservoir, and in 7.8% of bream fry in Zegrze Reservoir (Table III). Bream with two rows of pharyngeal teeth is more frequent in dam reservoirs than in rivers and lakes.

There are no literature data on the presence of specimens with teeth placed in one row in white bream. My studies revealed that such fish were very scarce in the Zegrze and Sulejów reservoirs.

Eastman and Underhill (1973) studied intraspecies variations of tooth formulae in 42 species of American cyprinids from the Leuciscinae subfamily. They stated that:

- teeth of the second row were usually less functional than of the main row;
- an extra tooth added to the formula typical of a species, appearing in the second or third row, was usually smaller and less specialised (its shape was different from that of other teeth in the row);
- an additional tooth appearing in the first row increased masticating potential;
- the appearance of an extra tooth was more frequent than the lack of a tooth;
- in the case of asymmetric tooth formulae, the additional tooth usually appeared in the left arch (so that the left arch had more variants of tooth formulae).

Only the first four statements were confirmed in this study. The last one was not confirmed, neither here not in the studies by other authors, with the exception of bream from Lake Dabie (Table V). The first three statements were confirmed for white bream, and the fifth one was confirmed partly both in this study (Sulejów Reservoir), and by other authors (Krzykawski and Gawliñski, 1986; Vasarhelyi, 1958) (Table VI).

A variety of hypotheses were formulated to explain deviations from a typical tooth formula in the investigated cyprinids. Eastman and Underhill (1973) suggested functionality (lack of teeth usually occurs in the secondary less functional rows, while the number of teeth in the main row either does not change or increases) and evolutionary trends as responsible for these changes (evolutionary trend in cyprinids reduces the internal teeth). Evans and Deubler (1955) stated that disturbances of tooth replacement were responsible for the anomalies in tooth formulas. Golubcov and Ilin (1983) suggested that atypical tooth formulas were an effect of intraspecific, and possibly also intrapopulational variability.

Table V. - Comparison of tooth formulas in *Abramis brama* (L.) from different water bodies.

	Vistula River		**Biebrza River**		**Dabie Lake**		**Seliger Lake**		**6 lakes from Poland**		**Kujbyshevsk Reservoir**		**Zegrze Reservoir**		**Sulejów Reservoir**		**German waters**		**Hungarian waters**	
Tooth formula	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
1.5 - 5.1							10	2.0			14	1.9	1	0.7	5	2.9	2	1.0		
1.5 - 5.0					4	8.3	15	3.0			36	5.0	2	1.4	7	4.2	11	5.5		
5 - 5.2											1	0.1								
5 - 5.1							28	5.6			53	7.2	3	2.1	10	6.0	6	3.0		
6 - 5	3	0.3							11	2.1			1	0.7			19	9.5		
5 - 6									2	0.4										
5 - 5	1001	95.4	53	88.3	40	83.4	447	89.4	457	92.1	628	85.8	137	95.1	143	85.1	162	81.0	275	100
5 - 4	19	1.8	7	11.7	4	8.3			9	1.9					3	1.8				
4 - 5	24	2.3							17	3.5										
4 - 4	2	0.2																		
Σ n	1049	100	60	100	48	100	500	100	496	100	732	100	144	100	168	100	200	100	275	100
Source	Tadajewska, 1981		Witkowski, 1984		Krzykawski and Gawliñski, 1986		Shutov, 1967		Tadajewska, 1980		Lukin, 1971		Present study		Present study		Miaskowski, 1958		Vasarhelyi, 1958	

A number of authors observed viable hybrids of bream with white bream, and of bream and white bream with other cyprinids (Berg, 1949; Nikolyukin, 1952; Rutte, 1962; Zhukov, 1965; Gasowska, 1968; Pushkin, 1971; Witkowki and B3achuta, 1980; Swinney and Coles, 1982; Kutuzov, 1983; Blachuta and Witkowski, 1983/1984; Witkowski, 1984; Fahy *et al.*, 1988; Economidis and Wheeler, 1989; Pitts and Cowx, 1992). These authors performed detailed comparisons of the anatomic and meristic characters in the hybrids and their parental species. Values of these characters were always intermediate. This applies also to arch shape, tooth formula and structure. The tooth formula of the hybrids of bream with white bream was 5-5.1, 1.5-5 (Witkowski, 1984), or 1.5-5.1 (Nikolyukin, 1952; Zhukov, 1965; Sappo, 1976). Gasowska (1968) examined hybrids of bream with roach and found that 55.9% of the arches had tooth formula 5-5 (typical of bream), and 39.5% had the formula typical of roach. Crosses of white bream with rudd showed the same trend (*op. cit.*): 26.7% had the formula typical of white bream, *i.e.* 2.5-5.2, and 36.7% that of rudd, *i.e.* 3.5-5.3. Due to frequent occurrence of natural crosses of bream it was hypothesised that bream with two rows of teeth must have originated from hybrids (Zhukov, 1965; Pushkin, 1971; Tryapicyna, 1979; Swinney and Coles, 1982). The hypothesis on the relationship between hybridisation and anomalies in tooth

Table VI. - Comparison of tooth formula in *Blicca bjoerkna* (L.) from different water bodies.

	San River		**Dabie Lake**		**Zegrze Reservoir**		**Sulejów Reservoir**		**German waters**		**Hungarian waters**	
Tooth formula	n	%	n	%	n	%	n	%	n	%	n	%
3.6 - 5.2									2	1.0		
3.5 - 5.3					1	0.7						
3.5 - 5.2			1	2.8	1	0.7	2	1.0	2	1.0		
2.5 - 5.3					1	0.7			1	0.5	1	0.1
2.5 - 5.2	60	96.7	23	63.9	98	73.1	175	89.4	170	85.0	682	99.3
2.5 - 5.1			3	8.3	7	5.2	6	3.0	8	4.0	1	0.1
2.5 - 5											1	0.1
2.5 - 4.3											1	0.1
2.5 - 4.2			1	2.8	4	3.0	3	1.5	4	2.0		
2.5 - 4			1	2.8								
2.4 - 5.2					2	1.5						
1.5 - 5.2			3	8.3	9	6.7	7	3.6	10	5.0		
1.5 - 5.1	2	3.3	4	11.1	7	5.2	2	1.0	2	1.0	1	0.1
1.5 - 4.1									1	0.5		
5 - 5.3					3	2.2						
5 - 5					1	0.7	1	0.5				
Σn	62	100	36	100	134	100	175	100	200	100	6,87	100
Source	Rolik, 1987		Krzykawski and Gawliński, 1986		Present study		Present study		Miaskowski, 1960		Vasarhelyi, 1958	

formula seems to be confirmed by the fact that bream specimens with two rows of teeth are most frequently found in dam reservoirs, where crosses are also more numerous. As observed by Witkowski (1984), many characters of bream and white bream hybrids remain within the range of variability noted for their parents. This renders precise species identification more difficult and possibly leads to many errors.

The hypothesis on the hybrid origin of bream with two rows of teeth was tested by electrophoretic studies on proteins (Golubcov and Ilin, 1983). The authors excluded the possibility that bream with two rows of teeth, which originated from a dam reservoir, was a hybrid of bream with white bream in the first generation (F_1). They also rejected the possibility that variations of tooth formula were due to hybridisation of bream with white bream having taken place in the past, but they were not too categorical in this respect. However, earlier studies had revealed that the method used by these authors was little effective in establishing the F_2 generation and backcross hybrids (Brassington and Ferguson, 1976).

It has been found that there is a period in bream ontogenesis when the fish possess two rows of teeth (Bielogurov, 1957; pers. data). Taking this into account, as well as the assumed evolutionary trend within cyprinids to eliminate the internal rows of teeth (Eastman and Underhill, 1973), it can be hypothesised that the occurrence of a teeth placed in two rows is the effect of an "unfinished evolution". If this were so, frequency of bream with teeth placed in two rows should be more or less similar in all habitats. Hence, it is difficult to explain why such fish are much more frequent in dam reservoirs. Dam reservoirs have been constructed at most some tens years ago. To attain such a high variability of tooth formulae in this brief period, when two rows of teeth are observed in as many as 20% of the population, there must have been some very "rapid" cause. Hybridisation may be such a cause, not so much between genetically pure lines of the two species, but rather between crosses of bream with progeny of some earlier backcrosses of white bream with bream, or even of white bream with other cyprinids. According to Shutov (1969) white bream is a species least susceptible to changes, and among the four cyprinids (*Blicca bjoerkna, Abramis brama, A. sapa, A. ballerus*), it is characterised by the least advanced evolution of pharyngeal teeth. Hence, if hybridisation really took place between bream and white bream, it would oppose the general evolutionary trend towards reduction in numbers of tooth rows.

It seems that at present there are too few data available to definitely reject one of these hypotheses. Deviations from the typical tooth formula in natural populations are probably due to a number of causes. The problem still requires a more definite explanation.

Similarities in arch shape observed in bream and white bream in early stages of development, the presence of teeth placed in two rows during bream ontogenesis, similarities in tooth shape of adults of the two species, and viability of their hybrids support Hensel's (1978) and Howes' (1981, 1991) suggestions that the two species should be included in the same genus.

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